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## The Scottsdale Conference on Neural Modelling

On April 11-15, 1983, a tutorial conference on neural modelling was held in Scottsdale, Arizona. The conference was supported by the Air Force Office of Scientific Research, by the Office of Naval Research, and by Arizona State University. The conference was organized by Peter Killeen and David Hestenes of ASU, and by Robert Hecht-Nielsen of TAMU, Inc. The principal speaker was Stephen Grossberg, Center for Adaptive Systems, Boston University. The goal was to provide a clear and concise exposition of the major concepts, themes and results of neural modelling, and to explore its implications for associated psychological disciplines. The format devoted the mornings to lectures by Grossberg on his theory of neural networks, and the afternoons to presentations by invited participants who also worked on neural models, or who generated empirical data pertinent to the predictions of those models. The following reviews and abstracts will provide you with an idea of the issues discussed in relation to neural models that week. (Sawyer)

# AN INTERDISCIPLINARY APPROACH TO BRAIN-BEHAVIOR DYNAMICS: SELF-ORGANIZATION OF INDIVIDUAL BEHAVIOR IN RESPONSE TO ENVIRONMENTAL CONTINGENCIES

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This work is divided into four interacting parts that explain and predict data from a wide variety of disciplines and paradigms. In the first part, a theory of perceptual and cognitive development is suggested. A central concern of the theory is the stability-plasticity dilemma: How can a system's adaptive mechanisms be stable enough to resist environmental fluctuations which do not alter its behavioral success, but plastic enough to change rapidly in response to environmental demands that do alter its behavioral success? How does a system distinguish between behaviorally important and irrelevant events? What is the processing unit that embodies this distinction? The stability-plasticity problem arises in a broad range of phenomena including perceptual adaptation, critical period termination, and attentional processing.

It is shown how a small number of design principles and mechanisms work together to achieve the stability-plasticity balance. These mechanisms include laws of competitive dynamics in feedforward and feedback (STM) networks, laws of adaptive learning (LTM), and laws of opponent processing expressing the action of tonically aroused, slowly accumulating chemical gates in competing network channels. It is shown how these mechanisms can be joined together to regulate the dynamic buffering of established representations and a rapid parallel search process leading to establishment of new internal representations. These processes are regulated by a competition between attentional and orienting subsystems within the network that are differentially activated by expected and unexpected events.

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This competitive structure leads to unified mechanistic explanations and predictions about such varied phenomena as: event related potentials, notably processing negativity, mismatch negativity, and P300; termination and chemically-mediated reversal of environmentally sensitive critical periods; Korsakoff amnesia data; item recognition data; and perceptual data; notably the McCulloch effect and rivalry. A central theme of the theory is that matching of bottom-up data with top-down learned expectancies, or templates, helps to dynamically buffer developing representations, and that a resonance process subserves the recognition event during which new adaptive changes can occur.

This general framework is articulated within a series of specialized theories. One theory derives associative learning laws for interactions between STM traces and LTM traces in a neural network. Developed over the past two decades, this theory anticipated and unifies information processing concepts such as unitized nodes, automatic activation of content addressable nodes, spreading activation, priming of STM, probes of LTM, hierarchical cascades, and distinctiveness. The theory shows how postulates about the adaptive self-organization of individual behavior in response to environmental pressures leads to a unification of specialized performance models, provides a physical interpretation of formal constructs in these models, and extends the predictive range of these models to include cross-checks of their concepts using interdisciplinary experimental paradigms.

A review is given of some recently confirmed theoretical predictions from the 1960s, notably that a UCS can modulate presynaptic conditioning of transmitter in a CS-activated pathway via a  $Ca^{++}$  current, and that transmitter production is inversely proportional to synaptic terminal size in a certain class of synapses. Laws for transmitter production, release, mobilization, gating, potentiation, and adaptation are derived from the associative laws. It is shown that brief, temporally spaced input pulses can lead to an explosive enhancement of activation in pathways wherein a single prolonged pulse can lead to an activation decline. This property is used to discuss kindling and the non-Hebbian nature of the associative laws.

It is mathematically demonstrated that the functional unit of associative learning in the networks is a spatial pattern of activation that is distributed across network nodes. General theorems about the design constraints needed to guarantee unbiased pattern learning by simultaneously active sampling sources are described. These design constraints subsume many of the specialized associative models in the literature. The theorems are applied to explain data about eidetic memory, top-down template learning, and synchronized performance of the elementary motions in a motor synergy. It is shown how complex preprocessing of signals, notably via dendrites, refractory periods, modulatory signals, and state-dependent thresholds influence the course of learning.

The associative laws are used to explain classical data about serial verbal learning and paired associates, notably the bowing and skewing of the serial position error curve, the form of the error generalization gradient at different list positions, the distribution of item and order information in STM through time,

and various backward learning effects. The form of the serial position curve is predicted to change in a prescribed way under parametric increases in arousal level, say due to amphetamine, and this result is compared with attentional deficits of certain overaroused schizophrenics.

It is shown that the temporal order properties in LTM that arise during serial learning have functional analogs in cognitive processes whereby command chunks governing planned behavior are self-organized. These processes are suggested to be a resonance phenomena, evolving serially in time, that helps to regulate the stability-plasticity balance. The rules for updating command chunks on a moment-by-moment basis contribute to a solution of the "assignment of credit" problem.

The simplest form of command hierarchy is described. This avalanche structure is used to organize data concerning command networks for motor control in invertebrates, performance speed-ups due to learning, competition between arousal sources as a mechanism of rapid switching between alternative behaviors and conditioning of cues to arousal sources as one mechanism whereby such cues become conditioned reinforcers.

Another specialized theory concerns the classification of mass action competitive systems, notably the types of pattern transformations executed by on-center off-surround networks undergoing shunting, or membrane equation, dynamics. This classification helps to solve the noise-saturation dilemma that afflicts all cellular systems; namely, the possible breakdown of sensitivity in these systems at both low and high background activity levels. The theory shows how mass action competition automatically retunes the sensitivity of the network as background activity levels fluctuate. Properties of feedforward competitive networks include reflectance processing above an adaptation level, Weber law modulation, featural noise suppression (suppression of zero spatial frequencies), pattern matching, shift property, edge detection, curvature detection, and outward peak shifts. These properties help to explain such perceptual phenomena as brightness constancy, brightness contrast, and angle expansion, as well as such cognitive phenomena as the redundancy of ratio scales and overlapping generalization gradients to decision making.

Feedback competitive networks enjoy a STM capability with remarkable properties. The classification of these properties include rapid parallel choice making, categorical perception, tunable filtering, multistable equilibria, hysteresis, contrast enhancement, masking, normative drifts, behavioral contrast, temporal order information in STM, standing waves, travelling waves, bursts, and chaos. These formal properties contribute to explanations of a wide variety of phenomena, including complex data about word recognition and speech processing; free recall without a serial buffer; automatic and controlled processing using a unified parallel mechanism; progressive sharpening of old memories; subliminal STM priming; attentional gating; read-out of terminal motor maps; von Restorff effects; decoupling of LTM order information from performance rhythm; filling-in reactions triggered by the matching of statistical edges, leading to global representations of binocular form that physically explicate the Fourier theory of spatial vision and reconcile feature extraction and Gestaltist approaches to binocular perception.

anatomical information theory and to networks wherein classical and instrumental conditioning mechanisms modulate and are modulated by attention switching events. This theory mechanistically explicates notions of reward, punishment, drive, incentive motivation, frustration, and orienting processing in a psychophysiological, neurophysiological, and pharmacologically predictive framework. A Gedanken experiment concerning the synchronization problem of classical conditioning leads to the main results.

The following types of phenomena are addressed: polyvalent cortical cells that are sensitive to the sum of CS and UCS effects; cortical conditioning by anodal D.C. potential shifts; conditioning of nonspecific arousal for diffuse modulators; secondary conditioning; emergence of late nonspecific waves during discrimination learning; appetitive and satiety drive inputs; thalamo-cortical and hypothalamo-hippocampal interactions in the evaluation of stimulus-reinforcement contingencies; sensitivity of self-stimulation to drive state and cue availability; latent learning; nonchalant asymptotic avoidance; discrimination learning by animals simultaneously deprived of food and water; positively reinforcing effects of unexpected shock reductions; Valenstein effect; schedule-induced polydipsia; flattening of generalization gradients by high motivation; peak shift and behavioral contrast; overshadowing; learned helplessness; relationship of RNY to incentive motivation; thalamocortical rhythm; amnesia due to hippocampal lesions; motivational baseline and hysteresis; meal prolongation by conditioned reinforcing cues; drive competition; hippocampal seizures; satiation-deprivation effects; momentary maximizing and reinforcement matching tendencies; exponentially weighted moving averages; inverted U in conditioning as a function of CS-UCS delay; conditioned emotional responses and avoidance response; difference between intraspecific drinking and normal drinking; attentional focusing, unblocking, and dishabituation by unexpected events; superconditioning; self-primitive behavior; and cholinergic-dopaminergic interactions during eating and drinking.

Of special importance to the theory is its 1972 model of opponent processing, which uses the gating actions of slowly varying, tonically arranged chemical modulators in competing channels to explain many properties that go beyond the predictive capabilities of more recent opponent processing models based upon simple subtraction of two variables. Notable among these properties are antagonistic rebound properties that replace drive reduction habituation, and tolerance-withdrawal properties in specialized applications. The opponent process model also exhibits inverted U properties that include distinct underaroused and overaroused depressive syndromes. An underaroused syndrome is suggested to occur in juvenile hyperactivity, Parkinsonism, and hyperphagic eating. Some continued predictions of this syndrome are noted and other predictions made. Overaroused properties are suggested to occur in some schizophrenics and in response to some analgesic agents.

Multiple roles for the hippocampus are suggested by the theory and are used to reconcile data about hippocampal conditioning, motor mapping, vigilance, and attentional feedback control.

properties of the CMV, P100, and motor potentials are used to support this discussion. Discrimination learning data concerning trigger jacking in response to oriented lines on a board of enclosed keys are explained, and predictions about CMV and P100 should vary during these discriminations about learning tasks are made. Another prediction suggests that application of 6-OMDA at a neurophysiologically testable opponent process site will spare the conditioning but prevent offset of the conditioned cue from having a positive reinforcing action.

## MECHON-LIKE ADAPTIVE ELEMENTS THAT CAN SOLVE DIFFICULT LEARNING CONTROL PROBLEMS

ABRAHAM -- NABTO, Computer and Information Science Department, University of Massachusetts, Amherst, Massachusetts

My research explores the relationship between properties of animal learning and computational methods for solving fundamental problems of knowledge acquisition. I show that there are specific and striking parallels between certain details of animal learning behavior and problem solving methods developed by engineers and computer scientists solely to solve difficult practical problems.

Parallels are drawn between stimulus context effects in classical conditioning and algorithms that orthogonalize stimulus patterns for associative storage, between the anticipatory nature of classical conditioning and an approach to the "assignment of credit" problem, and between bacterial chemotaxis and search strategies for problem solving.

Data are presented from computer simulation of a learning system, one whose design embodies some of these principles. The system is able to solve a difficult learning control problem. The task is to balance a pole that is hinged to a movable cart by applying forces to the cart's base. This classical control task is difficult because we assume that there is no knowledge of the cart-pole dynamics, that there is no pre-existing controller that can be imitated, and that evaluative feedback is not very informative. The system consists of a simple Associative Search Element (ASE) and a (rad) Adaptive Utility Element (ACE). In the course of learning, the ASE constructs associations between input and output by searching under the influence of reinforcement feedback, and the ACE constructs a more informative evaluation function than reinforcement feedback alone provides. I show that this system greatly outperforms other learning systems applied to this task, and argue that the methods are readily extensible.

Finally, I discuss the relationship between this approach and other attempts to solve problem solving neuron-like elements, and the possible implications of my work for research in the neurosciences. In particular, I discuss possible implications of the use of neuron-like adaptive elements that individually embody very sophisticated adaptive problem-solving methods.

# ON THE SPECIFICATION OF CODING PRINCIPLES FOR VISUAL IMAGE PROCESSING

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In this date a number of mechanisms have been proposed to operate when we observe, discriminate or detect images which are briefly displayed. In this presentation I deal with these processing units in some detail and propose a unified Coding Theory (UCT) which incorporates such mechanisms, being parsimonious with both receptive field and perceptive field profiles. Some consideration is given to image processing under transformations and the involvement of linear and non-linear processing characteristics of the above mechanisms.

## GATED DIPOLLS

GAIL A. CARPENTER, Department of Mathematics, Northeastern University, Boston, Massachusetts 02215

This lecture reviews some basic ideas from the theory of gated dipoles (S. Grossberg, Math. Biosci. 15 (1972), 253-285). The theory begins with the question: What is the simplest rule governing unbiased signal transmission between cells? The answer that the outgoing signal (T) should be directly proportional to the incoming signal (S) ignores the fact that transmission is mediated by a depletable chemical transmitter (z) which gates S. My mass action, then,  $T = Sz$ , where

$$\frac{dz}{dt} = \lambda(z-z_0) - Sz, \quad (1)$$

The transmitter slowly accumulates toward its maximal level (N) and is depleted by the incoming signal (S). T exhibits a transient overshoot in response to a sudden increment of S and a transient undershoot in response to a sudden decrement of S.

So far, when the input (S) is off, then the output (T) is also off. Now, then, could the offset of a cue such as light or shock drive an action? A gated dipole accomplishes this. A gated dipole consists of a competing on-cell/off-cell module with slow gates, tonic arousal (I), and phasic input (J). In the simplest feedforward anatomy, the undershoot in the on channel (fear, for example) caused by the offset of a shock (J) leads to a transient rebound in the off channel (relief).

Other experiments may be simulated, and predictions made, using only elementary algebra. For instance, with a linear signal function, a sudden arousal increment greater than a fixed size rebounds all dipoles in a field, independent of their J values; the size of the rebound increases with the size of J. Parametric experiments, varying either J or J, allow one to compute the signal function, f. A threshold-linear or sigmoid f has a characteristic underaroused syndrome, in which the dipole is insensitive to small J; is hypersensitive to larger J; and, with sudden arousal increments, can enhance overshadowed cues (d-shabitation). There is also an "inverted U" in the steady on reaction, with the dipole insensitive at both small and large arousal levels. In another context, reducing shock level from J to J/2 is shown to be 100% rewarding then reducing shock from J to 0.

# PHOTORECEPTORS AND CIRCADIAN RHYTHMS

GAIL A. CARPENTER, Department of Mathematics, Northeastern University, Boston, Massachusetts 02215

The elements which constitute a gated dipole may be rearranged and augmented to form a large class of models. Two examples from this class are presented in this lecture. In each case, mathematical and numerical analysis of model properties has been used to simulate a variety of experiments involving photoreceptors and circadian rhythms. Both projects were carried out in collaboration with Stephen Grossberg.

The gating model of photoreceptor dynamics, and hence of the transduction of light into an electrical response, provides a relatively simple alternative to the Baylor-Rodghia-Leeb blocking/unblocking model. With the inclusion of enzymatic activation, our transmitter laws form a minimal model for an unbiased miniaturized transduction scheme which can be realized by a depletable transmitter.

The gated pacemaker model of circadian rhythms is a behaviorally, physiologically, and anatomically predictive model of how these rhythms are generated by the suprachiasmatic nuclei (SCN) of the mammalian hypothalamus. Solutions of the model quantitatively fit much of the circadian data on activity that is thought to be controlled by the SCN. Examples include long-term after-effects, split rhythms, ablation studies, characteristic phase response curves, and Aschoff's rule for nocturnal and diurnal mammals. In order to explain all these phenomena, the basic gated pacemaker is augmented to include a metabolic feedback term ("fatigue") and a slow gain control process, which buffers the rhythm against short-term fluctuations in light level.

## EXPERIMENTAL DEMONSTRATION OF "SHUNTING NETWORKS," THE "SIGMOID FUNCTION," AND "ADAPTIVE RESONANCE" IN THE OLFACTORY SYSTEM

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My work and Grossberg's offer a striking case history of what happens when two investigators, one theoretical working from the top down, the other experimental working from the bottom up, meet on mathematical ground. Our commonality holds in particular at the later stages of sensory processing and the earlier stages of perceptual processing. I will comment on three basic features of his model: the "feedforward shunting network," the "sigmoid" input-output function, and the feedback network with "adaptive resonance." I will use these to illustrate the developments, modifications and re-interpretations required in order to realize a working physiological model within the general theory.

The experimental work has been done over the past two decades on the vertebrate olfactory system (Shepherd, 1972; Freeman, 1975, 1981). In many respects the olfactory bulb is the simplest, most accessible, and best understood part of the brain devoted to higher information processing, yet it manifests transformations

of sensory input that have been described in other sensory systems. This concurs with Grossberg's intent that his theory hold more broadly than for vision.

A "shunting network" operates in the outer layers of the bulb, which receives axon terminals from the olfactory receptors. This operation has been identified as "presynaptic inhibition" (Minor et al., 1969); however it is not merely presynaptic, and it is not inhibition in the classical Sherringtonian sense, because it is multiplicative and not additive.

The operation is mediated by a pool of interneurons in the outermost cellular layer. They are mutually excitatory and form what I have called a Kie set (Freeman, 1975). A transient excitatory perturbation of these neurons induces a surge of activity that long outlasts the transient and attenuates the transmission of receptor input to the bulb. The agent of attenuation is non-synaptic and probably involves the release, accumulation, and slow clearance of a substance such as potassium in the extracellular space in this synaptic layer.

Strictly speaking, this subsystem is not a "feedforward" network, because the degree of attenuation depends on the induced interneuronal activity and not directly on the input. Yet the overall operation yields the desired properties of range compression and signal normalization, in a manner formally related to Kushnir's (1965) prescription for accommodation in the visual system. Clearly such a mechanism is essential at or near the first central station in every sensory pathway, including the olfactory, in which the input to a glomerulus might be carried by from one to 20,000 axons, depending on odor type and concentration. Analogously, in simulating the operation of the bulb with nonlinear differential equations (Freeman, 1979b) it is necessary to employ a Kie set with an output that attenuates the simulated input to the inner bulb, in order to avoid saturation and instabilities of the inner subsystem.

The Kie set has other functions as well. It clips and holds the input from a sniff. It provides a degree of contrast enhancement by the extension of the attenuation effect from each local domain into its surround. It has a stable mutually excitatory state that provides a steady excitatory bias to the inner bulb, maintaining the inner bulbar subsystem in a quasi-linear domain. It compensates for surges in activity levels of inhibitory interneurons in the inner bulb that are induced by inspiration (Gonzales-Istrada & Freeman, 1980). The Kie set also has a zero stable state. In theory the transition from the high to the low state can be induced by a single inhibitory pulse, and can be reversed by a single excitatory pulse. This property might serve as a means for rapidly switching the bulb "off" and "on." However, no means for experimental demonstration of the requisite inhibitory centrifugal pathway has yet been found.

It is remarkable that these many janitorial functions of range compression, bias control, and the taking of local spatial and temporal integrals and derivatives should be executed by a single population of interneurons, prior to the real work of pattern recognition. These operations are more clearly or complexly manifested in other sensory systems; inevitably they are the first to be encountered by physiologists working

inwardly from receptors. On the whole they are well understate as types of sensory preprocessing. As Grossberg notes, the extrapolations to "feature detectors" and "frequency extracts" should be regarded with skepticism.

The existence of the "sigmoid function" for olfactory neural sets was predicted from the properties of bulbar electrical activity and was demonstrated experimentally by computing the probabilities of neural axonal pulses conditionally on amplified dendritic potentials (Freeman, 1975). An equation describing this function has been derived in part from the Hodgkin-Huxley system (Freeman, 1979a). It may well provide for the bulb the properties of noise suppression and signal enhancement described by Grossberg.

Three aspects deserve brief mention. First, this function is collective property and does not hold in this form for single neurons. Second, it is a major determinant of the global stability of the olfactory bulb. Third, the maximal slope of the curve is displaced to the excitatory side of the rest potential of the abscissa. This means that input not merely excites the bulb; it increases the global interaction strength. Thereby the inner mechanism changes with each inspiration from a quasi-equilibrium state to a limit cycle state and then back again.

The inner mechanism is formed by excitatory and inhibitory neurons with mutual excitation, mutual inhibition, and negative feedback comprising a Kie set, which is related (loosely speaking) to Grossberg's "dipole." The output of this set to the next cortical stage is a "wave packet" having a carrier frequency of 40-80 Hz and a duration on the order of 0.1 sec. The repetitive state transition with respiration is the key process leading to the self-organization property of the bulb manifested in these bursts of activity.

Hereby is revealed the phenomenon of "adaptive resonance." Information is carried by the wave packet in the patterns of amplitude and phase modulation of the carrier wave in its spatial dimensions. These patterns develop in part in respect to the initial conditions at the onset of the state change induced by inspiration, but in larger part in respect to intrinsic synaptic connections formed during prior experience (Freeman & Schneider, 1982). These spatially patterned connections, together with centrifugal controls, serve to define the "expectancy" that is being "matched" in some sense (not correlation) with the spatial pattern of input (Freeman, 1979c).

In serial pictures of bulbar spatial patterns of activity reconstructed by computer graphics (Freeman, 1973) one can "see" Grossberg's FIRE ignite and spread with each inspiration. Significantly, these "waves" do not propagate; they are standing waves that wax and wane over the time-envelope of the wave packet, while the filling in takes place.

There are numerous differences and uncertainties to be dealt with between theory and data. The experimental difficulties of precise description and measurement are taxing. However, there is no question that here is a robust convergence of theory and experiment that tells us we are on the right path.

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- ### INCENTIVE THEORY AND NEURAL MODELS
- PETER R. KILLEEN, Department of Psychology, Arizona State University, Tempe, AZ 85287
- It is possible to put some of the assumptions of Incentive Theory (Killeen, 1982) onto those that Grossberg has derived as essential components of his theory of neural networks. The most basic assumption of Incentive Theory is that the delivery of incentives excites an animal, and that an aroused animal engages in numerous locus-specific appetitive responses, including goal-tracking and sign-tracking. A second important assumption is that the rate of decay of arousal is not constant, but depends on the rate of an internal clock (Killeen, 1984). At asymptote, the time constant for the clock is about ten to twenty times as long as the interreinforcement interval that the animal has been experiencing. The time constant converges on that asymptote slowly, however, as an exponentially-weighted average of the current and previous intervals.
- With some cheating and sanding these assumptions dovetail nicely with those of Grossberg. For Grossberg, arousal occurs when there is a mismatch between expectancy and outcome, and this arousal causes the network to sample other templates--to "choose" other interpretations of the events. Grossberg also posits a separate incentive motivational arousal that permits sampling of potential cues, and permits the most predictive to themselves become conditioned incentives. However, I believe that this arousal might be based on the perceptual/expectancy-discrepancy
- tion arousal.) Now does the arousal generated by a perceptual mismatch relate to my incentive generated arousal? The latter occurs in situations of frequent, repeated, and highly predictable reinforcement, and is manifest in the agitated and energetic behavior of the subjects. What is the mismatch that might, in Grossberg's scheme, underlie the arousal? I suggest that the Pavlovian, sign-tracking conditioning that occurs in the moments before the delivery of the incentive generalizes throughout the interval. The effectiveness of the environmental stimuli as good predictors near the end of the interval, but not earlier in the interval, is the source of the mismatch. In Grossberg's theory time would normally enter as a compound cue (mediated by a neural "avalanche"), so that no expectations would be generated early in the interval. This may be happenier but temporal discrimination being imperfect, ample room is left for the "nervous expectation" seen in the interim. Other templates are being tried, and we call them adjunctive behavior.
- A fundamental design problem for neural networks is that of amplification of signals above the noise level without amplifying so indiscriminately that the system saturates. This problem motivated Grossberg to include normalization of the activity of a field of neural units as a basic part of his theory--an inclusion with several important secondary benefits, such as Hebb's law and contour enhancement. The adaptive internal clock that I use in my theory to accommodate the partial reinforcement extinction effect also provides a type of normalization. It is not designed a priori to keep the animal's behavior from "saturating"; in fact, the very slow adaptation of the clock causes animals in transition from low to high rates of incentive to be intemperate, even frenetic, in their activity. But eventually the animal will equilibrate, and it will do it on the basis of the real time rate of incentive. Behavior rates will thereby be adjusted above their floor and below their ceiling in most situations. This not only implies a solution (albeit a somewhat slow one) to the noise-saturation dilemma, it predicts that the lowering of the adaptation level by periods of time-out from reward will enhance responding during time-in (behavioral contrast), with explicit numerical predictions that differ as a function of the training histories of the subjects. I am just now beginning to test these models of transient and permanent contrast.
- The congruences in our theories represent convergent solutions to similar problems, and may be a source of further insight. In the best of situations, the constructs may become so similar that it will be parsimonious to presume that they label different manifestations of the same phenomena.
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THE AVIONIC'S LABORATORY ADAPTIVE NETWORK RESEARCH  
PROGRAM: AN OVERVIEW

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In this extramural and intramural research program, we are investigating single neuron and neural network models both theoretically and experimentally. The ultimate objective is to apply these models in the development of artificial intelligence. One approach we are focusing on is to view the single adaptive or plastic neuron as a goal-seeking system in its own right. In this view, neurons are postulated to have their own goals and their own adaptive mechanisms for learning to pursue these goals. Within this theoretical framework, brains are viewed as goal-seeking systems composed of goal-seeking components. This approach, with its emphasis on local neural mechanisms as the basis for memory, learning and intelligence, is currently being assessed by experimental and theoretical means. Results are presented from research at UC, Irvine, UCLA and the University of Massachusetts at Amherst.

LOCAL AND GLOBAL CONTROLS ON NEURAL PLASTICITY: THEORY AND EXPERIMENT.

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I describe some recent work from our laboratory on the principles that underlie neural plasticity in visual cortex. Included is a mathematical model for selectivity development in single neurons and experimental methods to analyze the global effect of certain neuropharmacological agents.

A model for selectivity maximization in single neurons has been developed based on simple assumptions of synaptic modification [1]. The theory is based on competition between patterns of activity rather than between synapses. The instantaneous change in synaptic efficacy is positive or negative depending on whether the stimulus pattern evokes a response that is respectively above or below the neuron's "modification threshold," so that strong patterns get stronger and weak ones weaker. This is expressed as a product of the afferent activity and a nonlinear postsynaptic modulatory function. Computer analysis shows that the model neuron develops to achieve maximum selectivity in any pattern environment. Furthermore it is in agreement with the results of a wide variety of deprivation experiments. A complementary model for selectivity minimization is put forward to complete a theory describing generalization and discrimination by single neurons.

An effort has been made to clarify the role of norepinephrine (NE) as a global modulator of plasticity in cat visual cortex [2,3]. Kittens that have undergone cortical depletion of catecholamines were subjected to monocular deprivation. The neurotoxin 6-hydroxydopamine (6-OHDA) was delivered in two ways. Application by osmotic minipump (as in [4]) was effective in preventing the usual shift in ocular dominance. Systemic neonatal injections of 6-OHDA had no noticeable influence on ocular dominance; however HPLC analysis showed that both

methods were highly effective in reducing cortical levels of NE. Possible reasons for this difference are discussed.

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A DISTRIBUTED ASSOCIATIVE MEMORY MODEL

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A distributed associative memory (DAM) model was discussed. Unlike many current passive network models which use discrete storage (nodes), many interconnections (links), nonoverlapping memory traces and a serial search process for retrieval, DAM uses distributed (redundant) storage, parallel processing, direct access (no search), and composite (superimposed) memory traces. It covers the memory processes of encoding, storage, and retrieval, and applies to item, associative, and serial-order information. The measures it describes or predicts are accuracy, latency, and confidence for both recall and recognition.

The general assumptions of DAM are that items can be represented by features, that convolution is the storage mechanism and correlation is the retrieval mechanism, that performance (both recall and recognition) depends on the similarity between the retrieved information and the target information, and the decision system governs latency and confidence. By considering features as random variables, one can use probability theory to develop expressions for the mean and variance of the similarity distributions. From this one can compute a signal-to-noise ratio to provide an overall measure of the capabilities of the system. Equating for storage capacity, a comparison of DAM with LAM (the Linear Associative Model by James Anderson) shows that DAM has a greater signal-to-noise ratio than LAM, and the difference increases as the storage capacity increases.

A UNIFIED ACCOUNT OF AMNESIA: RETROGRADE, ANTEROGRADE AND SPARED LEARNING

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Over the past several years a number of important results have been developing in the study of memory disorders. In particular it has been rather well established that there is a strong temporal gradient in retrograde amnesia in which most recent

marginal completeness. Satiation-deprivation processes can account for local (i.e., time-dependent) contrast effects.

Nevertheless, several questions remain unanswered: What is the proper quantitative form for these dynamic processes? Will the same form do for all activities? For the same activity under all conditions? What accounts for the transience of local contrast? Memory limitations seem to be involved because local contrast revives under conditions where stimulus identification or control is weakened. How do memory mechanisms relate to these short-term dynamic processes? Grossberg's dynamic equations may shed some light on these questions.

## ON THE "SOFT" CONSTRUCTION OF RHYTHMIC MOVEMENT: AN EXPERIMENTAL ANALYSIS FROM THE PERSPECTIVE OF A PHYSICAL BIOLOGY

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### 1. Hard Molded and Soft Molded Rhythmic Movement

Where explanations of rhythmic behavior such as locomotion have been neural in their focus the tendency has been to regard the behavior in question as hard molded (hard wired, hard gated, hard coupled, hard guided and hard algorithmed). The commonly proposed neural mechanisms, are single cells or ensembles of cells specialized for the generation of behavioral rhythmicities. A central pattern generator works, presumably, by guiding the chemo-electrical field along hard constraints (specific neural pathways linking specific neural elements) to produce periodic tensile states in the associated musculature.

Selverston (1980) has argued that understanding how a hard molded central pattern generator works for any given instance of rhythmicity requires identifying all of the ensemble's neural elements, all of the membrane and synaptic properties of those elements, and all of the connections among them. However, rhythmic motions of the body can be, and frequently are, soft molded (soft wired, soft gated, soft coupled, soft guided and soft algorithmed) which is to say that a biomimetic system with periodic behavior can be assembled temporarily and for a particular purpose from whatever neural and skeleto-muscular elements are available and befitting the task.

Both hard and soft construction of rhythmic movements must follow from principles that govern the cyclic mode of biological organization in general. In their basic format these principles are not likely to be unique to biology. Understanding the production of rhythmic movements that are softly molded from biological materials must rest on an understanding of the specific guesses assumed in distinct morphological settings by very general laws (cf. Iberall & Soodak, 1981). A program for understanding soft molded rhythmic behavior contrasts with that for hard molded rhythmic behavior in that it must give priority to physical law.

On at least two counts, it would seem that a law-oriented program is essential to the success of a neural-oriented program. First, there is the issue of how to rationally constrain the choice of relevant properties to be studied. Ideally, one wishes to

memory are most strongly affected and older memories affected less. This gradient lasts over a number of years. In addition, there is a strong correlation in patients with memory disorder between their ability to remember past events (retrograde amnesia) and their ability to learn new ones (anterograde amnesia). Finally, when a person is amnesic they can still learn and remember certain kinds of things. It has often been proposed that spared memory and learning abilities derive from different memory systems. We attempt to provide a unified account for all of these phenomena.

We began with the puzzle of how a superpositional memory system in which all knowledge is stored in a single set of synaptic weights could account for the temporal specificity of retrograde amnesia in which recent memories (within about two to three years) are selectively impaired. We propose an abstract account for this specificity and then propose a specific physiological mechanism which is consistent with our account and with the known constraints of the neurophysiology.

We embody this mechanism in a simulation model and show that it not only accounts for the temporal specificity of retrograde amnesia, but accounts for the general correlation between retrograde and anterograde amnesia. More importantly, we show that embedding our account in the framework of a superpositional memory allows us to give a natural account of spared learning effects within unitary memory mechanism.

### STATIC AND DYNAMIC COMPETITION

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The static, mutual properties of performance on multiple (successive discrimination) and concurrent (simultaneous discrimination) reinforcement schedules can be derived from four assumptions. (a) That inhibitory stimulus control--the suppression of an ongoing activity by presenting a stimulus--is associated with excitatory control of antagonistic activities: inhibitory control of activity A is excitatory control of complementary activity A'. The two complementary classes contribute to the terminal and interim activities observed in periodic-food experiments. (b) The competitiveness of an activity decreases as its level increases (diminishing marginal competitiveness). (c) That the competitiveness of an activity is inversely proportional to its rate of occurrence and directly proportional to its rate of reinforcement: (d) and that activities are in equilibrium when all are equally competitive. Matching, on concurrent VI VI schedules, deviations from matching, on multiple schedules, and behavioral contrast, together with the effects on contrast, of species, absolute reinforcement rate and response type, are all derivable from these assumptions.

These static, static relations must depend in some way on local, dynamic effects. The obvious possibility is that as an activity continues to occur at a high rate, its competitiveness declines and as time goes by without the activity, its competitiveness increases. A moment-by-moment satiation-deprivation process of this sort is the dynamic counterpart of static diminishing

manipulate those parameters of a central pattern generator that govern its operation. Unfortunately, the parameter set of a neural ensemble contains, by some counts, forty-six entries that could be relevant to a neurophysiological explanation (Muller, 1973). Principles beyond those of neurophysiology are required to guide the selection of parameters. Second, there is the issue of how to explain the characteristic quantities of a rhythmic behavior, for example, its period, amplitude and energy per cycle; these quantities cannot be rationalized on neural considerations alone.

## 2. The Pendulum, Clocking Mode

Locomotion must exhibit a limit cycle or clocking mode of organization insofar as the limb motions in locomotion are auto-oscillatory. Further, locomotion must exploit a pendulous-like mode of organization (interchanging kinetic energy) insofar as the limbs in locomotion are rhythmically raised and lowered under the influence of gravity. Both of these modes, the clocking and the pendulous, are simple dynamic regimes. And both can be soft molded. How does a complex system, dominated by plastic-elastic-gel processes simulate simple systems?

Understanding locomotion rests in part on understanding the physics that condenses out a simple pendulous, clocking mode in one limb and in a pair of limbs.

A typical experiment involves a subject who is swinging, out of phase by 180 degrees and at a common frequency, two hand-held pendulums of different lengths and masses. This is a case of coupling two "oscillators" of different natural periods. The coupled period is that which is the natural period of the pair as a single unit. As suggested by previous work on limb oscillations and their couplings, the natural periods of limb oscillations must be manipulable if the design principles of locomotion are to be uncovered (e.g., Graham, 1972; Shik and Orlovskii, 1965; Stein, 1977; von Holst, 1973). In our research, variation in natural period is achieved by variation in the length and the mass of the hand-held pendulums.

## 3. Among the results are these:

- (i) an isochronous pair of wrist-pendulum systems can be treated as a single virtual wrist-pendulum system of mass equal to the summed masses of the pair,  $\Sigma m_i$ , and of length equal to  $\Sigma l_i^2$ , by Huygens' law.
- (ii) the elected periods of single and paired systems are lavishly related to the moment variable  $(m/l^2)^{1/2}$ . This variable is arrived at a priori by dimensional analysis via a consideration of the mechanical constraints imposed by the type of biological system and by the function to be performed.
- (iii) the fact that the law applies to the virtual system defined by single quantities of mass and length implies that the nervous system is "transparent" to the conceived quantities.

- (iv) the data reveal the presence of a potential (a concentration of energy) in the paired case that does not exist in the single case. This potential is shown to be the energy for coordination, which is measurable. Across isochronous pairs, this energy measure varies.
- (v) Regarding the virtual system characterization as a "cooperativity," it is shown that the difference between the equilibrium state of the virtual system (qua a cooperative level) and the equilibrium state of the subsystems of which it is composed (qua an atomistic level) determines the energy for interaction or coordination.
- (vi) a generalized law of action is shown to apply. Action (energy/frequency) of a given wrist-pendulum system is constant across the various pairings in which it participates. The various pairings induce variations in frequency and amplitude.
- (vii) the law of action predicts that amplitude will relate parabolically to period. This is shown to be the case.
- (viii) action and natural period are independently determined. Action goes as the moment variable  $(ml^2)^{1/2}$ . Period goes as the moment variable  $(m/l^2)^{1/2}$ . Amplitude depends on both moment variables.
- (ix) generally speaking, a statistical mechanics/irreversible thermodynamics perspective on the assembling of rhythmic movements (as cooperative or coordination states) looks appropriate.